SOME DETAILS OF THE REPRODUCTIVE STRUCTURES OF SARCODES

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The genus *Sarcodes* includes but one species, *S. sanguinea* Torr., the snow flower, a fleshy, saprophytic plant common in the Sierra Nevada in California. This familiar plant has been described in detail by Oliver (6).

Each plant consists of a tuft of roots and a stout erect stem which bears spirally arranged scales. The abundant flowers are borne in the axils of the upper scales; the lower part of the stem may be regarded as a peduncle, and the upper as the rachis of a raceme. The stem, scales, pedicels and sepals are densely covered with multicellular glands. All parts above ground are brilliant crimson.

The flowers are ordinarily pentamerous. The sepals are separate; the petals are united for about half of their length and are entirely glabrous. The corolla and calyx are about equal in length; the tips of the petals curve outward while those of the sepals are slightly incurved. The stamens are ten in number, hypogynous, considerably shorter than the petals and slightly shorter than the pistil. The anther is about half the length of the entire stamen. The filament is ribbon-like, entirely glabrous, and attached to the outside of the anther a little below the middle. Dehiscence takes place by a pair of pores on the outer surface of the anther near the summit. The pistil is glabrous. The oblate-spheroidal ovary is marked by ten grooves in the planes of the filaments; at the base it bears a nectary with ten blunt lobes located between the grooves and projecting between the bases of the filaments. The internal cavity of the ovary is divided by five radiating septa located in the planes of the sepals and bearing massive placentae; in the lower part of the ovary the inner ends of the placentae are fused together so that the placentation is axile, while in the upper part they fail to meet and the placentation is parietal. The placentae bear a very large number of ovules. The cylindrical style, about as long as the ovary, is traversed by an open channel into which ridges, being upward continuations of the septa, project. The capitate stigma is five-lobed; the lobes are placed alternately with ridges which project into the style-channel: that is, they are the ends of the carpels.

We are able to amend or extend Oliver's description by observations of the vascular system of the receptacle, the structure and development of the stamen and the embryogeny. The observations are based on material supplied by Dr. Herbert F. Copeland, to whom we are most sincerely grateful. The material was collected at Jonesville, Butte County, at an altitude of 5000 feet, and fixed in Bouin's fluid. In making slides the usual microtechnical methods were employed and safranin and light green were used exclusively as the stains.

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Vascular Anatomy

The vascular tissue of the stalk—the peduncle and the rachis of the inflorescence—is to be interpreted as a cylinder, in which, however, the xylem is broken up into separate strands (Pl. 1, fig. 1). There is no sheath of fibers outside the phloem.[1] The departure of each leaf trace leaves one gap in the cylinder; the leaf trace is apparently to be interpreted as a single bundle but early in its course it frequently divides into two and before it enters the leaf breaks up into many. The vascular supply to each flower originates as two bundles, springing from the sides of the leaf-gaps just above the departure of the leaf trace; the two bundles unite in the cortex to form a cylinder, which enters the pedicel. In traversing the pedicel it breaks up into a ring of some five or six bundles.

As the bundles enter the receptacle (Pl. 1, fig. 2), a series of six whorls is given off in acropetal sequence: (1) a whorl of five sepal bundles; (2) a whorl of five bundles alternating with the sepal bundles, each of which splits tangentially into (a) several outer bundles that enter the corolla and (b) one inner bundle supplying an antipetalous stamen; (3) a whorl of five antisepalous stamen bundles; (4) a whorl of many carpel lateral bundles, arising on the inner sides of the bases of all the stamen bundles, and ascending the ovary wall; (5) a whorl of carpel dorsals ascending the ovary wall in the planes of the petal bundles; (6) a whorl of placental bundles in the planes of the sepal bundles. All the bundles in the ovary wall fade out just before reaching the style. The placental bundles enter the ovary in the planes of the septa and continue into and up the style. They fade out in the stigma.

The Stamen

In the youngest stamens we have seen, the relative sizes of the parts are about as at maturity; that is, the filament is rather

[1] "My statement [5] that there is a sheath of fibers in *Sarcodes* was based on inadequate observation"—(orally communicated by H. F. Copeland).

Explanation of the Figures. Plate 1.

Plate 1. Sarcodes sanguinea Torr. Fig. 1. Cross section of peduncle, ×4. Fig. 2. Half of a model of the vascular system in the receptacle, seen from the inside, ×16: *ca,* sepal bundles; *co,* petal bundles; *st,* stamen bundles; *cd,* carpel dorsals; *cl,* carpel laterals; *plac,* placental bundles. Fig. 3. Juvenile stamen, ×16. Fig. 4. Diagram of a longitudinal section of a stamen, showing the course of the vascular bundle, ×16. Fig. 5. Cross section through anther, showing pollen chambers at the plane represented by the line *a* in figure 4, ×40. Fig. 6. Mature stamen, showing open pores, ×16. Figs. 7, 8, 9. Cross sections of mature anther, the planes of which are represented respectively by the lines *a, b, c* in figure 6, ×40. Fig. 10. Cross section of anther wall, being an enlargement of the area marked by the dotted square in figure 9, ×320.

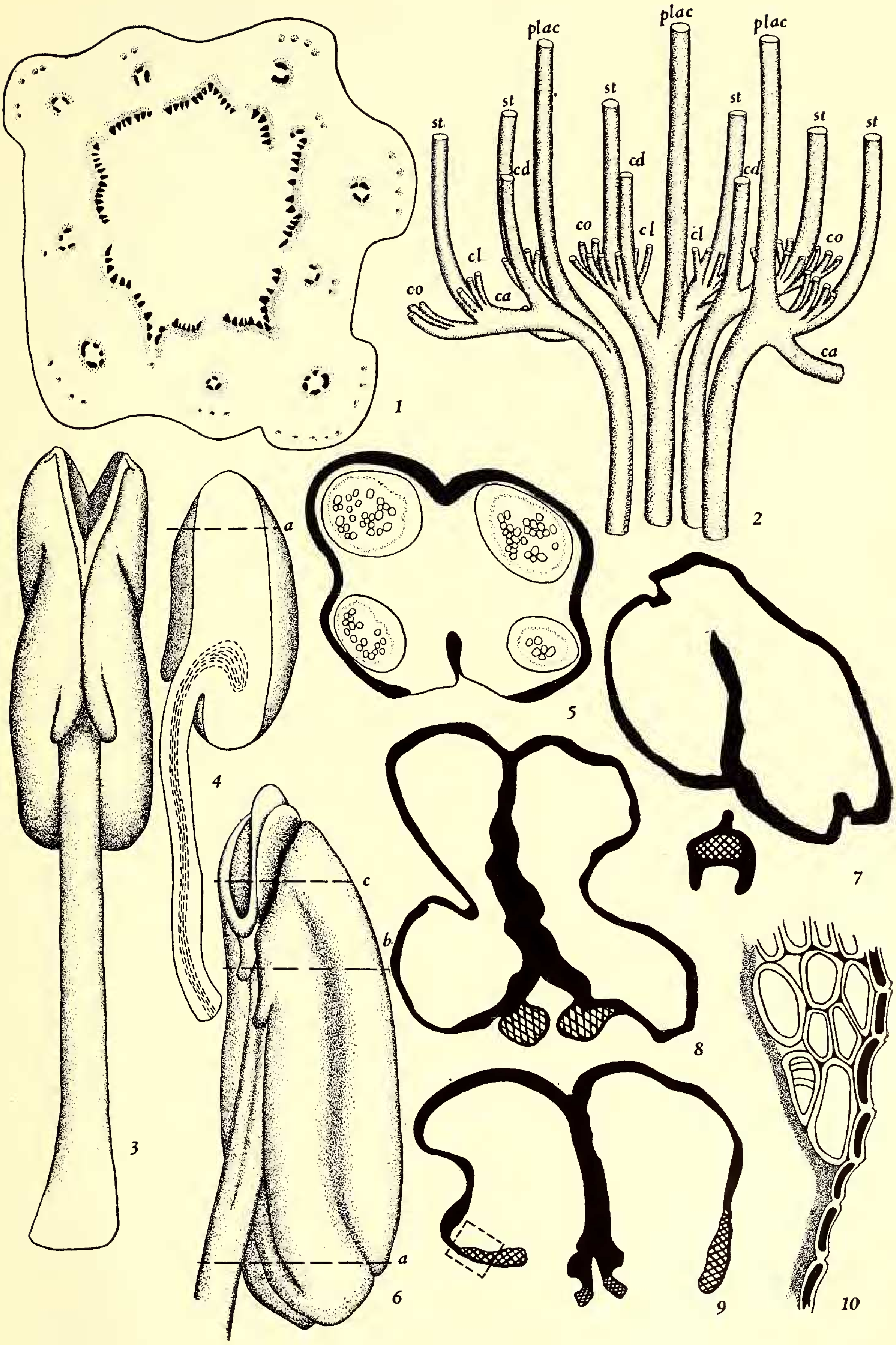

PLATE 1. SARCODES SANGUINEA TORR.

longer than the anther and enters on the outer side below the middle (Pl. 1, fig. 4). The stamen bundle bends so as to run not to the summit of the anther but to the lower end. The anther bears two rudimentary descending horns just above the insertion of the filament on the outside and below the pores (Pl. 1, fig. 3). In the young anther the usual four microsporangia with wall and tapetum are present (Pl. 1, fig. 5). The two pollen sacs on the inner side of the stamen extend somewhat nearer to the summit than those on the outside. The cells of the epidermis or exothecium are tanniniferous except for a patch on the outer side of the upper end of each anther lobe extending across the ends of the two microsporangia of the lobe where the pores are to form. In the youngest material we have examined the pollen grains had already formed. Most of them are four-grooved.

As the anther matures the wall between the two microsporangia of each lobe breaks down (Pl. 1, figs. 5, 7, 8); the connective (the wall in the plane of symmetry) also breaks down through a small part of its extent at the base of the anther; for the most part it persists. Where the pores are to form, and below them in the horns, a body of cells within the epidermis becomes differentiated by thick ribbed walls (Pl. 1, fig. 10). Dehiscence appears to be accomplished by a contraction of the exothecium which tears the body of thick walled cells in two by a lengthwise slit; the slit becomes a pore rimmed by thick-walled cells (Pl. 1, figs. 6, 9).

Embryogeny

The ovules have an integument of about four layers of cells. In the young ovule a few cells of the outermost layer show indications of tannin being present. Later, nearly all the cells of this layer are tanniniferous. The embryo sac develops in the manner usual in Sympetalae. The archesporial cell forms a megaspore tetrad. The spore at the chalazal end of the tetrad enlarges (Pl. 2, fig. 11); its nucleus undergoes three successive divisions which result in four nuclei at the chalazal end and four nuclei at the micropylar end. One nucleus from each end moves toward the center of the embryo sac; there these two nuclei unite to form the endosperm mother nucleus. Cell membranes form around the remaining six nuclei. The three resulting cells at the chalazal end are the antipodal cells. The largest of the three at the micropylar end is the egg and the other two are the synergids (Pl. 2, fig. 13). Meanwhile, the nucellus and the other three spores have disappeared. Following fertilization and before the embryo divides, the endosperm goes through a series of divisions. Each nuclear division is followed by cell division and the first two divisions produce a row of four cells (Pl. 2, figs. 14, 15). The second and third cells of this row (counting from the micropylar end)

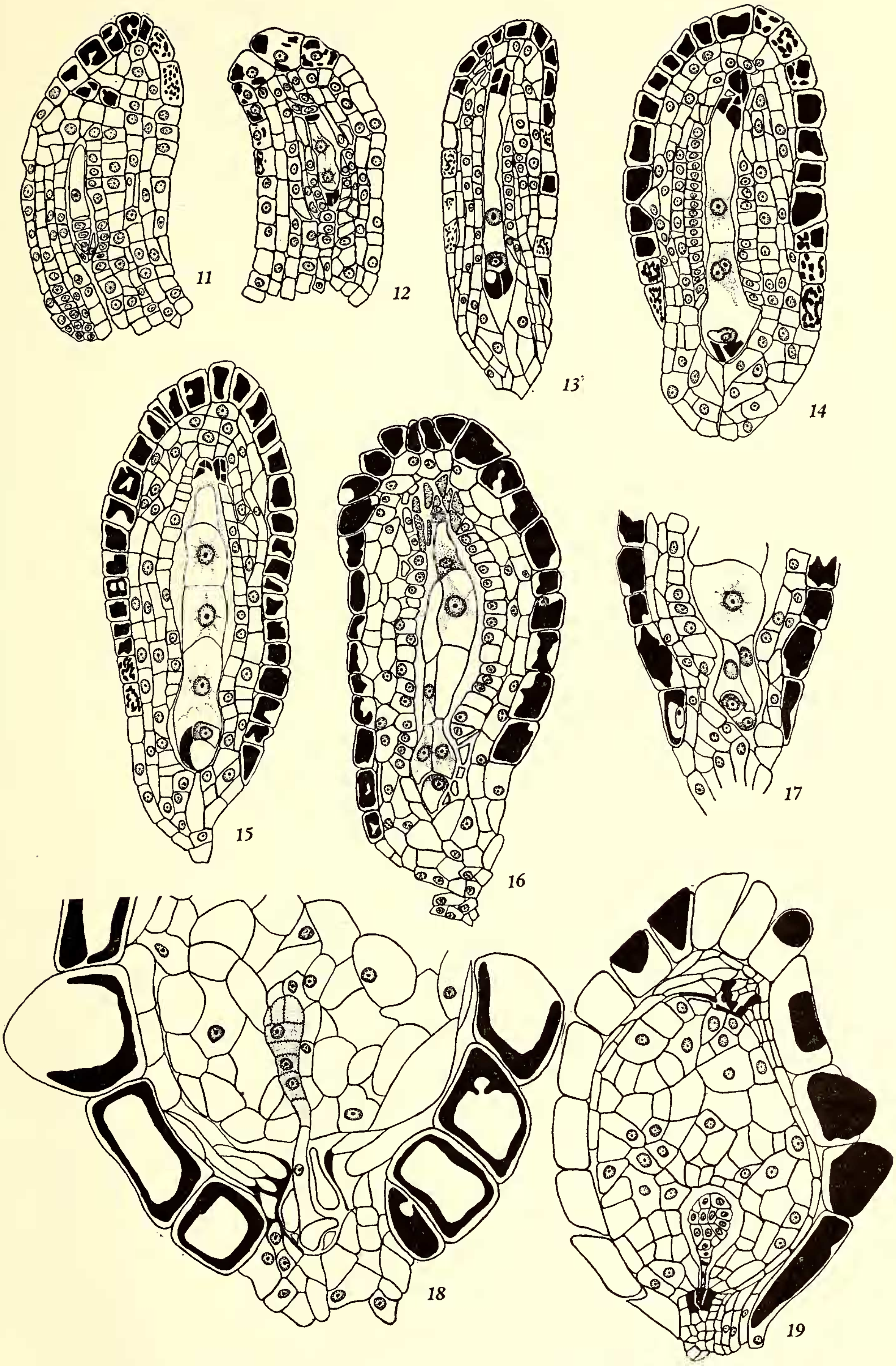

PLATE 2. SARCODES SANGUINEA TORR. Longitudinal sections of ovules and young seeds in successive stages of development. FIGS. 11–18, ×160. FIG. 19, ×80.

divide repeatedly and produce many cells while the first and fourth cells develop into haustoria (Pl. 2, figs. 16–19). At the same time the antipodal cells and the synergids disappear. The zygote first divides into two cells after the endosperm is past the four-celled stage (Pl. 2, fig. 17); of the two daughter cells of the zygote, the one toward the micropyle elongates and forms a suspensor. The suspensor carries its sister cell up to about the level of the wall between the first and second cells of the four celled endosperm. The original suspensor cell undergoes no divisions and grows no farther; its sister cell, by a series of divisions, adds to the suspensor, so that the summit of the embryo is carried in among the cells derived from the second cell of the four-celled endosperm. In this region a globular mass of cells, the definitive embryo, is developed (Pl. 2, fig. 19). By this time the integument has for the most part been absorbed, except for the outer layer of cells which have become thick-walled; the seed is essentially mature.

Discussion

Copeland (1, 2, 3, 4, 5) has made several contributions to the knowledge of the details of the reproductive structures of Monotropoideae. Our studies show that the details of the reproductive structures of *Sarcodes* are essentially in agreement with what he has found. The outer whorl of stamen bundles and the carpel-dorsals are in the planes of the petal bundles. The placental bundles are in the planes of the sepals. The embryo sac is normally developed and of normal type. In certain minor details of the development of the embryo, in which, according to Oliver's figures, *Sarcodes* is different from other Monotropoideae, we were unable to corroborate his findings; apparently *Sarcodes* agrees perfectly with other members of the group.

The integument of most Monotropoideae is of just two layers of cells and the endosperm is of but few cells. The four-layered integument and the mature endosperm of many cells in *Sarcodes* are distinctive characters of the genus.

The course of the bundle in the anther, running as it does to the base and not to the summit, shows that the end of the anther which is toward the base of the flower is the distal end and the end toward the summit of the flower is the proximal end. The stamen develops, in fact, with the distal end of the filament turned in and down, so that the outer, apparently dorsal, surface of the anther is in reality the ventral surface. This structure of the stamen seems to be typical of the order Ericales. The horns, found in many Ericales on the ventral surface of the anthers, are absent in most Monotropoideae, though conspicuously present in *Pterospora*. We think it significant that rudimentary horns, previously unreported, are present in *Sarcodes*.

The four-grooved pollen grains of *Sarcodes* are like those of

Pterospora and *Pleuricospora*. The pollen grains of *Allotropa* are three-grooved, while those of *Monotropsis* have two grooves.

Copeland (5) expressed the opinion that *Sarcodes* together with *Pterospora* and *Allotropa* make up the most primitive tribe of Monotropoideae, being the link between the Ericaceae proper and other Monotropoideae. The characters of *Sarcodes* as we have come to know them lead us to believe that this is the true conception of the line of evolution.

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A STUDY OF ISOETES IN SAN DIEGO COUNTY, CALIFORNIA

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Three species of *Isoetes* occur in San Diego County, California: *I. Nuttallii* A. Br., *I. Orcuttii* Eaton, and *I. Howellii* Engelm. To these species, eleven names or combinations of names have been applied at various times and the validity of at least one of them, *I. Orcuttii,* has been questioned by Norma E. Pfeiffer, the most recent student of the genus. (Monograph of the Isoetaceae. Ann. Mo. Bot. Gard. 9: 79–232. 1922.) In the present study ecological and morphological aspects of the genus are emphasized. The writer is indebted to Dr. A. W. Haupt and to Dr. Carl Epling, both of the University of California, Los Angeles, for suggestions.

The living material studied came from the Kearney Mesa which is about fifteen miles north of the city of San Diego and five to ten miles inland, and from a pool about eight miles farther north. This area is a table-land drained by a system of small streams which have running water only after rains. These streams retain occasional pools along their courses, eventually drying up completely during the long rainless period lasting from May until November or December. Between streams are low mounds covered with a chaparral vegetation, alternating with shallow depressions which retain water throughout the rainy season and in which many small hydrophytes flourish. A more detailed account of this region may be found in a recent article by